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Mode and causes for the Pleistocene turnovers in the mammalian fauna of Central Europe

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The Pleistocene mammalian fauna of Central Europe is characterized by a repeated exchange of glacial and interglacial faunal assemblages. The climatic oscillations caused a severe change of the geographic conditions, especially in Central Europe. Due to the shift of shorelines caused by the changing sea level and the massive ice shield over Scandinavia, Central Europe shifts from a highly continental climate during glacial periods to a maritime climate during interglacial periods. With regard to the mammalian fauna, humidity was a more significant climatic factor than temperature. Most of the larger herbivores reacted with immigration when the climate improves and local extinction when it deteriorates. For these species Central Europe is an 'area of temporal occurrence'. This repeated immigration was only possible due to 'core areas' nearby, where species survived continuously through the glacial cycles. The core area of the interglacial fauna is the Mediterranean and that of the fauna of the Mammoth steppe is situated in Eastern Europe and Siberia. Causes for final extinctions of particular taxa have to be sought in the core areas.

Die pleistozäne Säugetierfauna Mitteleuropas ist durch den starken Austausch zwischen warmzeitlichen und kaltzeitlichen Faunen gekennzeichnet. Die klimatischen Verschiebungen veränderten speziell in Mitteleuropa die geographischen Bedingungen. Durch die Verlagerung der Küsten als Folge der Meeresspiegelschwankungen und durch den Eisaufbau über Skandinavien lag Mitteleuropa während der Kaltzeiten in einem stark kontinental geprägten Klimabereich, während der maritimen Einfluss in den Warmzeiten dominierte. Die Feuchtigkeit war als Steuerungsfaktor biologisch bedeutender als die Temperatur. Die meisten grossen Pflanzenfresser wanderten ein, wenn das Klima für sie günstig wurde und starben lokal wieder aus, wenn sich das Klima verschlechtert. Für diese Arten bildete Europa stets nur ein 'temporäres Verbreitungsgebiet'. Die wiederholte Einwanderung war nur möglich, weil die Arten in der Nähe ihre 'Kerngebieten' hatten, in denen sie die glazialen Zyklen kontinuierlich überdauern konnten. Das Kerngebiet der warmzeitlichen Fauna lag im Mittelmeerraum und das der kaltzeitlichen Fauna der Mammut-Steppe in Osteuropa und Sibirien. Ursachen für das endgültige Aussterben müssen jeweils in den Kerngebieten gesucht werden.

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INTRODUCTION

Comparing the biostratigraphy of the Tertiary and the Pleistocene, both periods have a very different character, at least in Central Europe. During the Tertiary the mammalian fauna evolved much more continuously than during Pleistocene. While the Upper Tertiary can be divided according to the mammalian evolution into biostratigraphic zones of a duration of about 1,000,000 years, the Pleistocene is characterized by much more short-lived faunal changes. This is due to the severe climatic changes with cycles of roughly 100,000 years or less.

The biostratigraphic zones of the Tertiary are characterized by the FAD (First Appearance Date) and the LAD (Last Appearance Date) of significant species (Lindsay *et al.* 1990, Bernor *et al.* 1996). The occurrence of new taxa is mostly due either to evolution within a lineage or to immigration of new forms. The Pleistocene faunal changes in Central Europe, on the other hand, are characterized mainly by repeated immigration. Most of the major herbivores were not continuously present for a prolonged time span but disappeared and occurred repeatedly. This interrupted occurrence is due to ecological changes that did neither allow the glacial nor the interglacial fauna to survive in Central Europe. Thus, it is almost impossible to use the method of FAD and LAD for biostratigraphic purposes.

These basic facts are generally known but rarely are discussed in detail. The aim of this paper is to concentrate on two aspects of the Pleistocene faunal exchange in this part of the world. On one hand, geographic reasons are discussed why the repeated faunal exchange was more significant in Central Europe than in most other parts of the world. On the other hand, the mechanism of faunal turnovers will be reviewed in order to differentiate between areas of temporal and permanent occupation. This sheds new light on the Late Pleistocene extinctions.

CENTRAL EUROPE, A SPECIAL CASE?

After the discovery and general acceptance of the 'Ice Age', it took some decades until researchers became aware of the sequence of multiple glacial and interglacial periods during the Pleistocene. Central Europe provided the first evidence for a Pleistocene ice age as well as the first traces of the repeated climatic change during this period published in the classical work by Penck & Brückner (1907-1909). In consequence, glacial faunas with *Mammthus primigenius* and interglacial ones with *Elephas antiquus* could be attributed to cold and warm periods, respectively

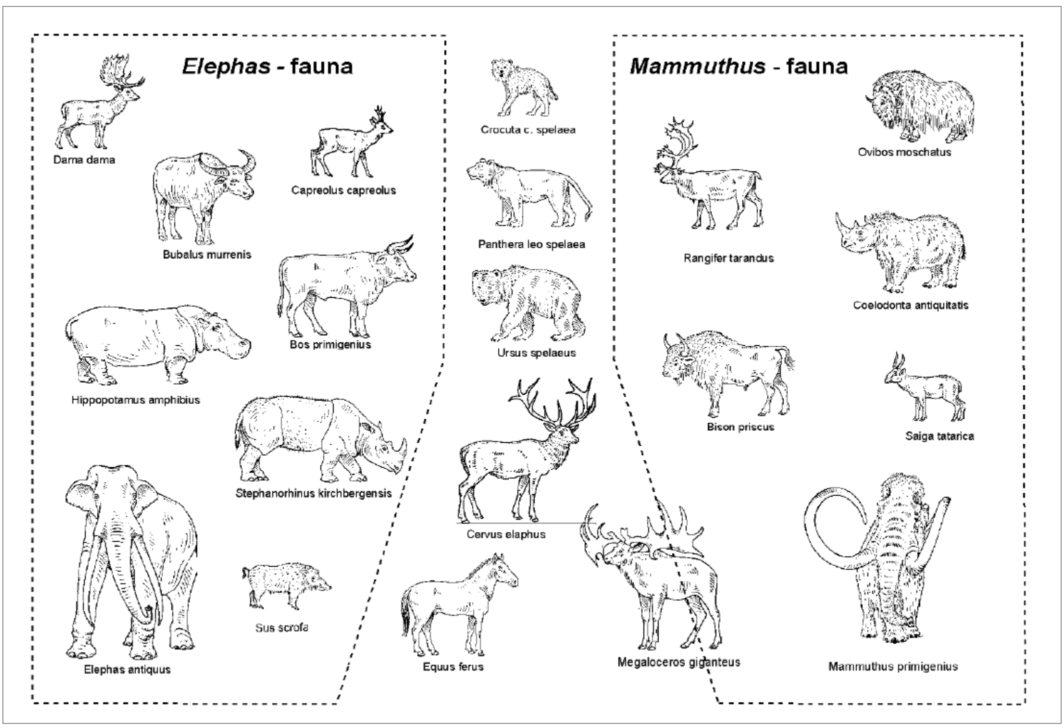

Figure 1 The mammalian fauna of Central Europe during the Late Pleistocene. Most of the larger herbivores belong either to the glacial faunal assemblage (*Mammuthus*-fauna) or to the interglacial faunal assemblage (*Elephas*-fauna).

(Koken 1912). In the meantime, we know from the deep-sea record that Pleistocene climatic history is much more complicated than envisaged in the classical scheme. Therefore, it is much easier to distinguish between cold and warm faunal associations than to correlate each of these with specific stratigraphic levels (Koenigswald & Heinrich 1996, 1999).

The contrast between glacial and interglacial faunas from Central Europe is best known in the late Middle and Late Pleistocene (Fig. 1). The interglacial periods are characterized by the *Elephas antiquus*-fauna which contains *Stephanorhinus kirchbergensis*, *Sus scrofa*, *Dama dama*, *Capreolus capreolus*, *Megaloceros giganteus*, *Alces latifrons*, and *Bos primigenius* in addition to the straight tusked elephant as important faunal elements. Under especially mild climatic conditions, even *Hippopotamus amphibius* and *Bubalus murrensis* occured (Koenigswald 1988).

During glacial periods the *Mammuthus primigenius*-fauna was present. Its typical species are *Coelodonta antiquitatis*, *Rangifer tarandus*, and *Bison priscus*, besides the woolly mammoth. In very continental conditions, the range of *Saiga tatarica* and *Ovibos moschatus* reached as far west as France. *Equus ferus* and *Cervus elaphus* are more or less equally distributed in both faunas. They are the only larger herbivorous mammals that do not show a distinctive preference for the one or other fauna. In contrast, most carnivores like *Crocuta crocuta spelaea*, *Panthera leo spelaea*, and *Canis lupus* do not show any preference for one of the faunas because they are not linked as tightly to a specific vegetation as the herbivores are. In Western and Central Europe, these two herbivore faunal types were more or less totally exchanged during each major climatic cycle. From the record of the deep sea (Imbrie 1985; Shackleton 1997), it is obvious that the changes in the temperature during the Pleistocene were global. Therefore, one should expect to find similar faunal turnovers in other parts of the world as well. However, this is definitely not the case because similar latitudes neither in North America nor in Asia show such faunal changes.

With regard to the Pleistocene fauna of Central Europe, Nehring (1880) already emphasized the steppe character of the glacial fauna, which is documented by the immigration of species now living in southern Russia such as *Allactaga major*, and *Saiga tatarica*. The occurrence of the high arctic *Ovibos moschatus* in these faunas indicates low precipitation. In contrast, some of the interglacial faunal elements, such as *Hippopotamus amphibius* and *Bubalus murrensis*, inhabited Western Europe and the Rhine area although temperatures were not much higher than in the Holocene. Their occurrence is only plausible if the maritime influence of the climate was distinctly greater than today, causing mild winters (von Koenigswald 1988). This indicates that - at least for Europe - the global changes of the temperature were only part of the factors determining the climate. Changes in humidity seem to have controlled the ecological conditions even to a greater extent than changes in the temperature.

These great changes in humidity were caused by the specific geographic conditions in Europe. During glacial periods, the sea level was lowered due to the ice concentrated on the continents. The English Channel and the shallow areas of the North Sea fell dry, and the coastline retreated to the north. The remaining waters in the north were largely covered with ice. In addition, the katabatic winds from the huge Scandinavian ice shield dried up Central Europe. Thus, the continental influence increased drastically. The dry and cold conditions even reached Western Europe leading to an expansion of the mammoth-steppe with its typical fauna westward into Central and Western Europe (Guthrie 1990).

During interglacial periods, on the other hand, when the sea level was roughly as high as nowadays, epicontinental seas embraced Central Europe in the north and formed a climatic buffer. Thus, the maritime influence reached further East. Its decline from the west to the east can be demonstrated by the distribution of some taxa from the interglacial *Elephas antiquus* fauna. According to the available fossil record from the Middle and Upper Pleistocene, *Hippopotamus* expanded its range in western Europe as far as 53° north and colonized the Rhine river system as its easternmost extent. *Bubalus murrensis*, so far known only from the Upper Rhine area and the Netherlands (Koenigswald 1988, van Dam *et al.* 1997, van Kolfschoten 2000, de Vos *et al.* 2001) may have populated a similar area. *Elephas antiquus*, well known from Western Europe, was obviously less sensitive. Its easternmost occurrence is near Warsaw (Jakubowski *et al.* 1968), but hardly further East (Markova 2000). This can be interpreted as a gradual decline of the maritime influence from west to east in interglacial times, similar to the gradient observable in the Holocene vegetation.

The main reason for the immense faunal exchange in Western and Central Europe is the drastic shift from the maritime to the continental realm and back. If in other parts of the world similar geographic conditions had occurred, a comparable faunal exchange might have happened there too. Even in Europe, the continental character of the climate was more continuous further to the east and thus the faunal exchange there was minor. In the Great Plains of North America or in Siberia, the continentality of the climate was dominant throughout most of the Pleistocene and therefore, most probable, the alternation of cold and warm phases did not affect the faunal assemblages in a similar way.

FAUNAL EXCHANGE

In order to understand the faunal exchange and its significance for the Late Pleistocene extinction some general ideas have to be discussed here. Under favorable conditions, mammalian populations constantly produce a surplus of offspring. This pressure of a slight overpopulation leads to an expansion of the inhabited area until specific limits are reached. For terrestrial mammals, such limits may be formed by geographic barriers such as mountain ranges or coastlines or by ecological barriers, mostly climatic in nature, or, more rarely by competing taxa. The two main aspects of climate are temperature and humidity. The critical values are not set by the annual mean values but by the extremes during the seasonal cycle. To some degree, mammals can avoid the extremes during summer or winter by migration. Seasonal migrations can be identified only rarely in the fossil record, however. Therefore, in the context of this paper, the range of a species includes its entire range during the various seasons.

Due to the climatic changes during the Pleistocene, the areas of most mammalian species shifted, expanded or shrunk. In order to understand the process of faunal exchange better not the species as a whole but the populations have to be considered. The area inhabited by a species is composed of the areas of populations. The marginal ones are of primary importance in case of climatic change (Fig. 2). If the climate improves, the marginal populations provide the surplus of young individuals who can immigrate into the newly inhabitable region, if the amelioration continues, they will establish new populations. If the climate deteriorates, again the marginal populations are affected first. The normal reaction to stress is the reduction of offspring, either by fewer animals being born or fewer juveniles surviving. If the deterioration continues for a longer time, the marginal populations will die off. In both cases, the populations located more to the center of the inhabited area are almost unaffected by the climatic change. The widespread (and somewhat anthropomorphic) assumption that animals under stress move to grounds that are more favorable requires uninhabited areas. However, in the mosaic of populations, most favorable areas are already occupied. Because only the marginal population experience the stress, while the others do not since the critical values of humidity or temperature are not yet

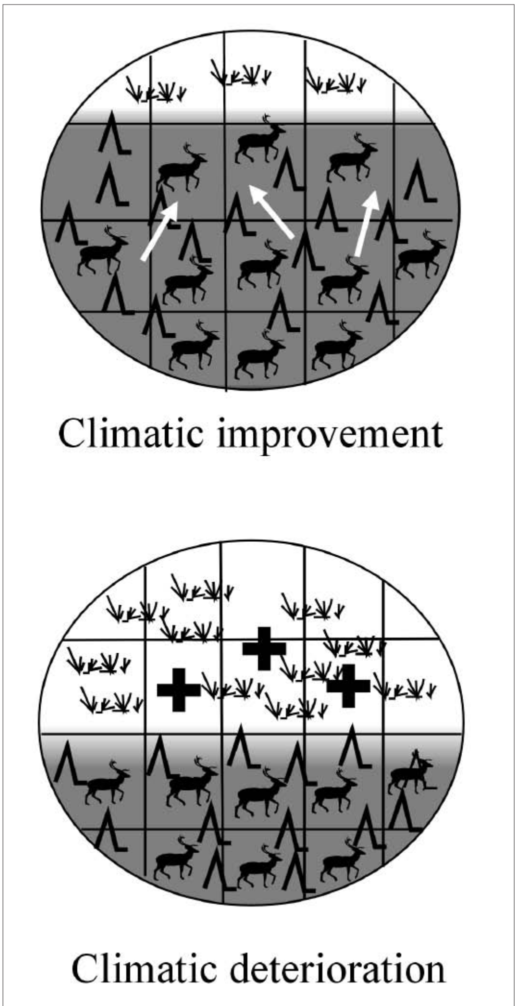

Figure 2 For the distribution of a species marginal populations play an important role during periods of climatic improvement or deterioration. In most cases, these populations cannot react to a climatic deterioration with 'emigration' a, but face local extinction.

exceeded, these populations might allow only single strong individuals to enter their territory but have no reason to move away or to share their territories with stressed populations.

Once a marginal population suffers local extinction because of prolonged severe stress, the next populations become marginal and may meet the same fate. Whether the entire species is affected, depends on the climatic deterioration reaching the entire area inhabited by the species.

The overall picture may sometimes resemble a general shift of area if the loss on one side is compensated by an acquisition in another. However, even here it is more probable that local extinction occurred on one side and immigration from marginal populations on the other. A general shift of all populations within the mosaic is unlikely. Although the climatic changes of the Pleistocene were global, they affected the composition of the mammalian fauna differently in the various regions. When the glacial fauna went extinct locally in Central and Western Europe, it survived in Eastern Europe and Asia during the warm periods. Similarly during glacial periods, the interglacial fauna survived in the Mediterranean. From there, the faunas reinvaded Central Europe when the climate was favorable again. Therefore Western and Central Europe was neither inhabited constantly by the herbivores of the glacial fauna nor those of the interglacial fauna.

For a better understanding of the mechanics of faunal exchange, it is useful to differentiate areas which were occupied by specific species almost continuously, and which might be called 'core areas', from those where certain taxa occurred only under specific climatic conditions. These can be called 'areas of temporal

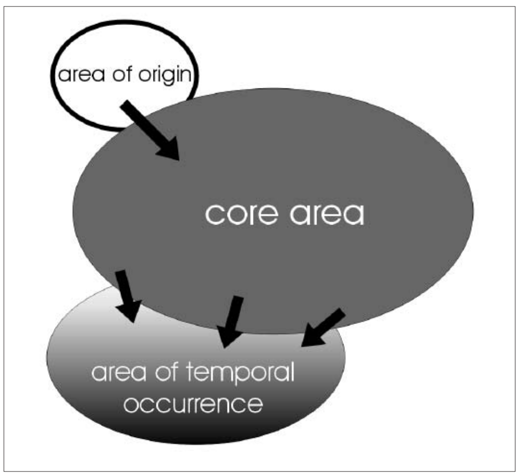

Figure 3 The repeated faunal exchange in Central Europe leads to the differentiation of areas of temporal occurrence and core areas, where species survive climatic oscillations. The core area is not necessarily identical with the area of origin.

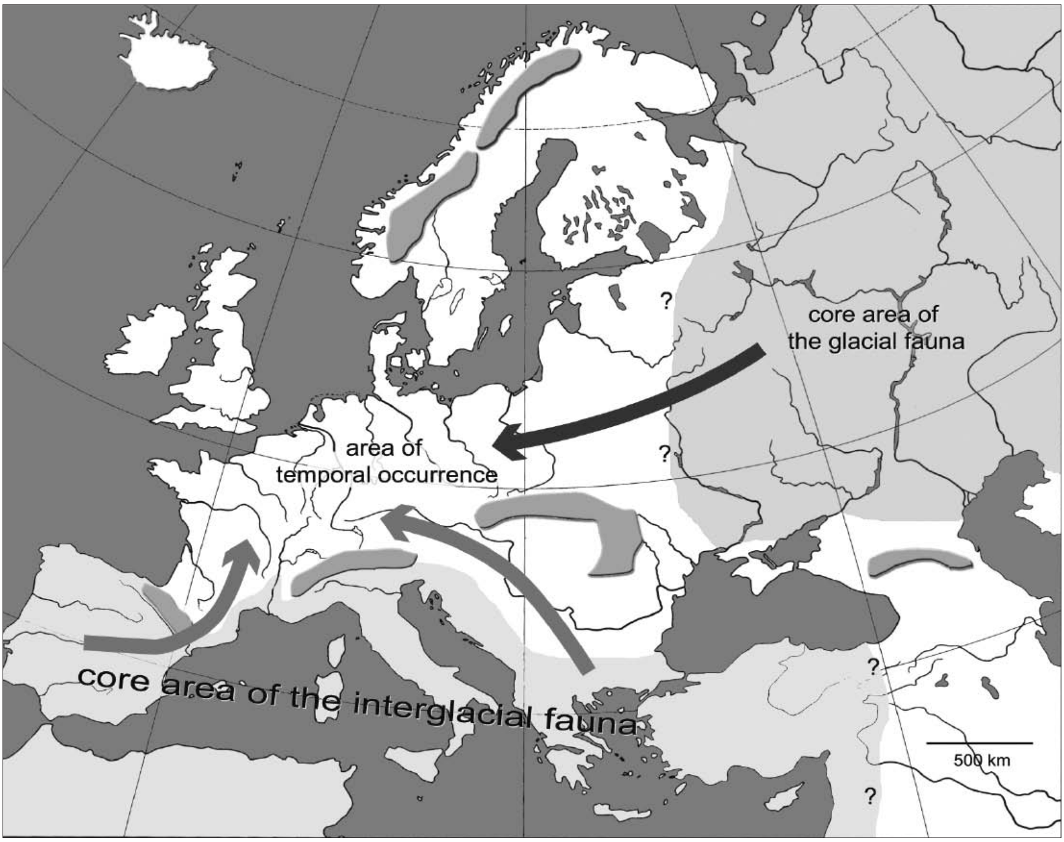

Figure 4 During the Middle and Late Pleistocene, Western and Central Europe were mostly areas of temporal occurrence. The glacial fauna of the Mammut-steppe migrated from its core area into Eastern Europe and Siberia. The interglacial fauna mostly came from the Mediterranean.

occurrence' (Fig. 3). On the European continent, both types are present. Western and Central Europe are typical areas of temporal occurrence. Neither the glacial nor the interglacial fauna could live there continuously. With each major climatic change, the local herbivores went extinct in this area and were replaced by new invaders coming from core areas where they had survived. Therefore, no continuous evolution of these species was possible in the area of temporal occurrence (Fig. 4).

In Eastern Europe and Siberia, on the other hand, climatic conditions were more stable due to the continental realm. Therefore, these regions formed the core area of the glacial fauna where it could survive interglacial periods. The Mediterranean formed the core area for the interglacial faunal elements. From there, interglacial faunal elements could re-invade Western and Central Europe as soon as the climate had sufficiently improved. Since the Alpine belt formed a geographic barrier, the immigration followed most probably the Rhone in the west and the Danube in the east.

The faunal exchange in Central Europe is very impressive during the Late Pleistocene and may have been less significant in earlier times. However, already early in the Middle Pleistocene, we find a repeated replacement among the elephants (Kahlke 1995, von Koenigswald & Heinrich 1999). Several sites in Thuringia provide an example of an early ecologically induced faunal exchange. *Mammuthus meridionalis* known from the

Early Pleistocene was replaced by *Mammuthus trogontherii* at the stratigraphic level of Sangerhausen but reoccurred in Voigtstedt, to be replaced by *Mammuthus trogontherii* again at Süssenborn. A similar alternative occurrence of these two elephants was documented for the Kärlich locality in the Rhine valley (Turner 1990; van Kolfschoten & Turner 1996). At higher levels, *Mammuthus trogontherii* and later *Mammuthus primigenius* take turns with the straight-tusked elephant, *Elephas antiquus*. The intensity of the faunal exchange increased during the Middle and the Late Pleistocene and included larger herbivorous mammals. Among the rhinos *Coelodonta antiquitatis* and *Stephanorhinus kirchbergensis* form a similar couplet, excluding each other. This repeated faunal exchange leads to a gradual decline in faunal diversity. The most significant sequence of faunal extinction happened during the Late Pleistocene (Koenigswald 1999). There is extensive debate whether humans are to blame for the extinction of the large herbivores during the Late Pleistocene. This question will not be discussed in detail here, but according to the distinction between core areas and temporally occupied areas made here, it becomes obvious, that hunting in Central Europe would not effect the species in their core areas. Although the archeological record is fairly dense, Central Europe was populated by only very few people (Zimmermann 1996, Koenigswald 1999), hardly enough to drive healthy populations of mammals to extinction. Only if the populations where already reduced by unfavorable climatic conditions, the last members may have been killed by humans. Haynes (1999) also limits the effect of early Indians on the North American mammoth and mastodon in this way. The main reasons for the final extinction have to be sought have in the core areas.

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